

Does nest luminosity play a role in recognition of parasitic eggs in domed nests? A case study of the red bishop

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Abstract Certain light environments may hinder egg discrimination by hosts of foreign eggs, which could in some circumstances lead to the acceptance of non-mimetic eggs by hosts. We measured light parameters at red bishop (*Euplectes orix*) nests and used a model of avian visual processing to quantify the detectability of eggs in the light environment in which they are perceived. We found that the overall amount of light was very variable between red bishop nests and always sufficient for colour discrimination. A model of avian visual processing revealed that nest luminosity had no influence on host responses towards eggs which were painted dark brown. Dark eggs do not appear to be cryptic in red bishop nests and can be distinguished with ease, whereas natural red bishop eggs are usually accepted, despite the domed structure of the nest. We found little variation in both chromatic and achromatic contrasts between host and artificial eggs, indicating that there was very little variation in the light quality inside nests. We suggest that nest luminosity is likely to play a role in egg recognition in situations when light reaches threshold values for colour discrimination, i.e. in scotopic as opposed to photopic vision. Rejection rates for dark eggs were higher than for bright (conspicuous) foreign eggs. More investigation of domed nest-building species is required, as this type of nest appears

to have a highly variable light environment, dependent on both nest structure and habitat.

Keywords Brood parasitism · Domed nest · Egg discrimination · Light conditions · Nest luminosity

Introduction

It is now over 20 years since the publication of Endler's seminal papers (1990, 1993) emphasizing the importance of variation in the ambient light environment on colour perception by animals. In the natural world, light environments vary continuously across space and time, causing changes in the conspicuousness of colours and patterns (Endler 1993). An animal's visual perception of an object is constrained on one hand by its own spectral sensory capabilities and on the other hand by the interaction between the spectral properties of the ambient light environment and those of the object itself. This investigative approach has since been applied in a variety of contexts in evolutionary ecology. In terms of sensory adaptations, birds have at least four spectrally distinct cone types (Bowmaker et al. 1997) and are sensitive to near-ultraviolet wavelengths to which humans are blind (reviewed by Bennett and Cuthill 1994). Cherry and Gosler (2010) have reviewed the implications of this and note the paucity of studies measuring eggs in their nests, as this environment, combined with specific properties of avian vision, is likely to influence the evolution of egg colouration.

Cherry and Bennett (2001) were the first to investigate the matching between avian brood parasites and their hosts using ultraviolet-visible reflectance spectrophotometry. They proposed the light environment hypothesis that certain light environments may hinder egg discrimination by hosts, which could under some circumstances lead to the acceptance of non-mimetic eggs by hosts. There is evidence (albeit based

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on museum specimens rather than field studies) that in cavity-nesting birds, discrimination based on achromatic characteristics could be important. Avilés (2008) compared the extent to which parasitic cuckoo eggs could be discriminated from eggs of two host species—the redstart *Phoenicurus phoenicurus*, which always nests in cavities, and the pied wagtail *Motacilla alba*, which can nest in crevices or holes—using Vorobyev et al.'s (1998) discrimination model to simulate host retinal function together with spectrophotometric measurements of museum egg collections. He investigated both colour matching and the role of nest luminosity on host perception of matching between eggs of hosts and six different genets of cuckoo eggs. He found that cuckoo eggs of the *Phoenicurus* gens showed better chromatic matching with redstart host eggs than did other cuckoo races and, in most cases, cannot be discriminated by hosts. By contrast, under dim light conditions, achromatic differences between cuckoo and host eggs can be distinguished easily, whereas the proportion of cuckoo eggs discriminated by chromatic signals was only marginally affected. Thus, nest luminosity has potentially far greater effects on achromatic than on chromatic matching.

The light environment hypothesis has been tested in the field by only two studies. Langmore et al. (2009) have shown that the dark eggs of Gould's bronze cuckoo *Chalcites russatus* are cryptic in the domed host nests which it parasitizes, whereas a congeneric bronze cuckoo species parasitizing red-capped robin *Petroica goodenovii* nests, which are open-cupped and have far greater ambient light levels, lays mimetic eggs. Honza et al. (2011), working on the open-cup nesting great reed warbler *Acrocephalus arundinaceus*, found that the interaction between ambient light levels and chromatic contrasts between host and cuckoo eggs predicted egg rejection, with chromatic contrasts being more detectable as ambient light levels increased. These studies show that the evolution of egg rejection defences in different host species may be significantly constrained by visibility in the nest.

In southern Africa, about 130 bird species build domed nests—the second most common nest type after open-cup nests, used by circa 200 species (Tarboton 2001) including several *Ploceid* hosts of the diderick cuckoo *Chrysococcyx caprius*. One of these is the red bishop *Euplectes orix*, a highly sexually dimorphic polygynous ploceid widespread in southern Africa which nests colonially. Males build between 10 and 15 nests per season and may have up to seven breeding partners. Females accepting male nests add a lining of soft grass to the inside cup of the nest, which has a single side entrance with an average diameter of 57 mm. Eggs are laid at daily intervals, and the female usually lays three eggs but can lay up to six; only she incubates the eggs and broods and feeds the young (Tarboton 2001). The various genets of the diderick cuckoo lay mimetic eggs in the nests of their respective bishop, sparrow and weaver hosts (Tarboton 2001); in the

red bishop, brood parasitism by the diderick cuckoo occurs at varying levels of intensity, between 0 and 60 % (Friedl 2004). The main factor appearing to influence brood parasitism is colony size, with small colonies experiencing higher levels of parasitism (Lawes and Kirkman 1996). Intra-specific brood parasitism has been recorded in 6.5 and 6.6 % of nests, respectively (Lawes and Kirkman 1996; Friedl 2004).

Domed nests are adaptive in reducing predation and in shielding eggs and nestlings from exposure to the elements (Tarboton 2001), but a potential cost associated with such an adaptive function could be a light environment in which it is more difficult for hosts to discriminate foreign eggs. The red bishop is an ideal candidate for such a study, as it builds a domed nest with a relatively small side entrance, but there is great variability in the nest wall structure, allowing different levels of penetration of light. Brown and Lawes (2007) suggest that the visibility in red bishop nests limits its ability to recognize eggs, so the primary objective of our study was to objectively measure the quantity and quality of light inside these nests and analyse the effect of nest luminosity on the rejection of parasitic eggs. To achieve this goal, we measured light parameters in nests and used a model of avian visual processing (Vorobyev and Osorio 1998; Vorobyev et al. 1998) to quantify the detectability of eggs in the light environment in which they are perceived (Endler 1990). We predicted that the interaction between nest luminosity and chromatic contrasts between host and parasitic eggs would affect rejection and, in particular, that dark eggs might appear cryptic.

Methods

Study area and experimental parasitism

Field work was conducted during September 2010 and 2012 at five colonies located in farmlands within a 20-km radius to the north and west of the suburb of Durbanville in the city of Cape Town, South Africa. Host nests were systematically searched for in littoral vegetation composed primarily of narrow-leaved cattail *Typha angustifolia*. All nests included in this study were found during the nest building or at the beginning of egg laying and were checked on a daily basis to monitor clutch size. Eggs were numbered with a felt-tip marker to indicate their position in the laying sequence.

In 2010, to assess rejection behaviour towards conspecific parasitic eggs, we parasitized nests ($n=19$) with conspecific red bishop eggs from other females, collected from abandoned nests during laying and kept in the fridge and used within a few days for experiment. In 2012, to test whether the light environment inside nests influence host reactions to parasitic eggs by rendering dark eggs as cryptic, we parasitized nests ($n=32$) with red bishop eggs painted (acrylic) a dark brown colour (Fig. 1). Conspecific eggs were chosen to

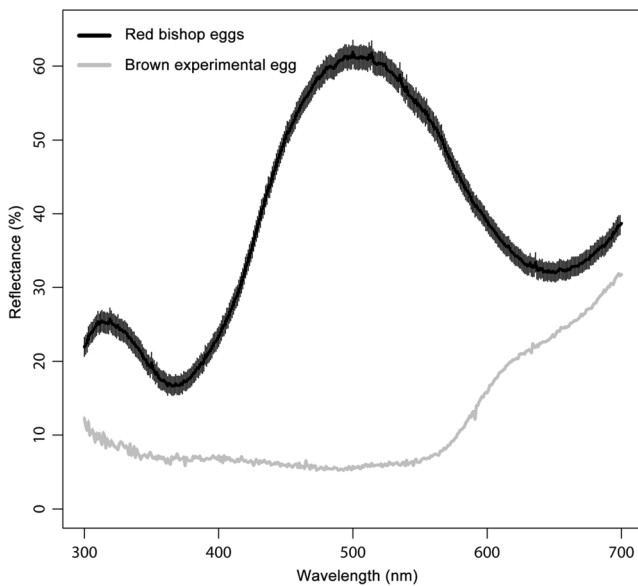


Fig. 1 The mean reflectance spectra of red bishop eggs ($n=19$) from seven females and experimental brown parasitic eggs ($n=10$). Bars denote standard errors of the mean

eliminate the possibility that eggs were rejected on the basis of egg size, which is the primary parameter used for rejection by cavity or dome nesters (Mason and Rothstein 1986; Marchetti 2000).

As red bishops exhibited quick rejection of parasitic eggs, experimentally parasitized nests were checked daily during the first 5 days after parasitism and later less frequently until hatching. If the egg did not disappear and the clutch was incubated, it was considered accepted and experimental eggs were removed from the nest. Otherwise, it was considered rejected (either ejected or deserted). Nest abandonment was regarded as a host response towards the parasitic egg because none of control nests ($n=25$) that were not parasitized but visited at the same frequency was deserted. In experimentally parasitized nests, we recorded nest abandonment only in one case, i.e. 4.2 % ($n=24$ rejections).

Reflectance measurements, luminance measurements and modelling of avian visual system

We measured spectral reflectance of the red bishop eggs and the light environment inside nests in 2012. Spectral reflectance of eggs was measured in the range of 300–700 nm (the spectrum range that birds can actually perceive, see Cuthill 2006) using a spectrophotometer (USB2000, Ocean Optics, Dunedin, FL) in a dark room indoors to avoid an effect of ambient light on spectrophotometric measurements. For measurements, we divided each egg into three regions across the longitudinal axis and took three measurements from each region (each covering ca 1 mm²). We avoided the egg poles to eliminate a possible measurement error owing to marked curvature of the eggshell surface. During measurement, the

illuminant was a deuterium and halogen light source (DT-Mini-GS, Ocean Optics). The light was transferred to the eggshell through a quartz optic fibre (QR400-7-UV/VIS-BX, Ocean Optics) with specially adapted probe for blocking ambient light at its end. The probe also ensured that the light was reflected at an angle of 45° from the eggshell. Data from the spectrophotometer were loaded into OOIBase32 (Ocean Optics) software. The measurements were relative and referred to a standard white reference (WS-2, Ocean Optics) and to darkness. Reference and dark calibrations were made prior to the measurement of each clutch.

The nest light environment was measured in situ at all experimentally parasitized nests ($n=32$). To characterize light conditions in the nests, solar radiation measurements between 300 and 700 nm were taken on the day of experimental parasitism around midday (between 11:00 and 14:00 CET). Light environment was characterized by photon flux spectra ($\mu\text{mol s}^{-1} \text{m}^{-2}$) calculated from absolute irradiance spectra ($\mu\text{W}/\text{cm}^2$) based on the procedure outlined by Endler (1990). We used photon flux because animal photoreceptors respond to photons independent of energy (Endler 1990). From these spectra, we also calculated the total intensity of ambient light in nests—the total illuminance ($\mu\text{mol s}^{-1} \text{m}^{-2}$). This variable was calculated as an integral of photon flux spectra in the range 300–700 nm. To control if the cloud cover significantly changes the light availability in nests, we compared total illuminance inside the same nests ($n=15$) on cloudy and cloudless days and found no difference (paired Wilcoxon test statistic=67, $p=0.7197$). Before measurement, a sensor was set to the hole of the nests and positioned horizontally parallel to the clutch facing towards the back of the nest. To take absolute irradiance spectra, we used a portable Jaz spectrometer (Ocean Optics) and optical fibre cable (QP400-2-SR-BX, Ocean Optics) with cosine corrector (CC-3-UV-T) which expands the fibre field of view to 180°. The Jaz spectrometer was calibrated every morning with a tungsten-halogen light source (HL-2000-CAL, Ocean Optics) of known absolute intensity values at wavelengths from 300 to 1050 nm.

To determine the degree of colour difference between host and experimental brown eggs in each red bishop nest, we used the Vorobyev-Osorio model for tetrachromatic vision (Vorobyev and Osorio 1998; Vorobyev et al. 1998) implemented in the Avicol program (Gomez 2006). The final outputs of this model were two contrasts, chromatic determining difference in hue (ΔS) and achromatic one determining difference in brightness (ΔQ). To calculate contrasts, we entered several variables into this model. They were photoreceptor spectral sensitivities, photon flux spectra from each nest and the mean reflectance spectra of host and experimental brown eggs (Fig. 1). There was very low variability between the reflectance of a particular egg of different females (mean reflectance=39.2 % \pm 2.55 [standard error of the mean], hue [wavelength of the maximum reflectance]=502 nm \pm 2, $n=7$). Therefore, we used mean egg reflectance from 19 eggs of

seven females for subsequent contrast calculations. Because of the very low variation in the colouration of blue bishop eggs (see also Lawes and Kirkman 1996), we believe that using mean reflectance spectra should not affect calculation of contrasts as much as illuminance in nests.

The red bishop belongs to the Passerida clade, and recent studies indicate that species in this clade possess UV type of colour vision (Ödeen et al. 2011). Therefore, we used blue tit (*Cyanistes caeruleus*) single- and double-cone sensitivities (Hart et al. 2000) for calculation of chromatic and achromatic contrasts, respectively. Because there was enough light in the nests (minimal illuminance was $101 \mu\text{mol s}^{-1} \text{m}^2$), we used the model incorporating neural noise only, independent of the number of absorbed spectra. Therefore, the Weber fraction (ω) was independent of light intensity and computed as follows:

$$\omega_i = v_i / \sqrt{\eta_i},$$

where v_i is the noise-to-signal ratio of a single cone (taken as 0.05) and η_i is the relative cone proportion (Vorobyev et al. 1998). We used relative proportions of cone types in the retina for a blue tit (UVS=1, SWS=1.92, MWS=2.68 and LWS=2.70; Hart et al. 2000). Both contrasts (ΔS and ΔQ) between both types of eggs are in relative values, just noticeable differences (JNDs). Essentially, higher values indicate higher colour difference between eggs (Vorobyev and Osorio 1998; Vorobyev et al. 1998; Gomez 2006). It must be noted that only quality of light expressed by the shape of photon flux spectra in the red bishop nests influenced the calculation of both contrasts.

Statistical analysis

To explore if the ambient light conditions may potentially affect red bishop responses, we fitted a generalized linear model (GLM) of a binomial logistic regression with binomial error distribution and a logit link function. Responses to the experimental brown egg were entered as a binary coded dependent variable (0 = acceptance, 1 = rejection).

Explanatory variables were chromatic and achromatic contrasts. Because there is some evidence that intensity of ambient light can influence rejection of experimental eggs even in photopic conditions (Honza et al. 2011), we also included in our analysis information about the intensity of ambient light in the nests—the total illuminance ($\mu\text{mol s}^{-1} \text{m}^2$). Thus, the initial model contained both contrasts (ΔS and ΔQ), total illuminance and all their interactive terms. Model simplification was performed by backward stepwise elimination of non-significant terms from the initial model based on the change of deviance between the full and reduced models tested by a χ^2 test (Faraway 2006; Crawley 2007). Statistical modelling was performed in R 2.14 (R Development Core Team 2012).

Results

The mean reflectance spectra of the red bishop eggs ($n=19$) were similar in shape, which is consistent with their blue appearance to humans; non-mimetic experimental eggs, by contrast, were brown (Fig. 1). The rejection of brown eggs was observed in 20 out of 32 cases (62.5 %). The light intensity was highly variable in nests: total illuminance ranged from 101 to $2650 \mu\text{mol s}^{-1} \text{m}^2$. However, this predictor did not explain host responses ($p=0.95$, Table 1, Fig. 2) and darker conditions probably did not hinder discrimination of these eggs. Neither ΔS nor ΔQ between brown and host eggs influenced host reactions ($p=0.52$ and $p=0.16$, respectively, see Table 1). JNDs did not differ between acceptors and rejectors in either chromatic (38.38 ± 0.05 [standard error of the mean] for acceptors; 38.35 ± 0.04 for rejectors) or achromatic (29.49 ± 0.15 for acceptors; 29.88 ± 0.19 for rejectors) contrasts. No interactive terms between predictors were significant ($p > 0.33$, Table 1).

Experimental parasitism with conspecific eggs showed different rates of rejection. Hosts rejected these eggs in only four out of 19 parasitized nests (21.1 %), and the difference in rejection rate between these two experimental groups was significant (Fisher exact test, $p=0.008$).

Table 1 The effect of measured variables and their interactions on the probability of egg rejection in red bishops. Only the minimum adequate model from logistic regression analysis is presented. p -values of particular terms come from final models after model simplification and are based on type III sum of squares. Degrees of freedom for all predictors are equal to 1

Variable	Estimates	Std. errors	χ^2	p values
Intercept	-2.07×10^3	3.63×10^3	–	–
Chromatic contrast	5.44×10^1	9.46×10^1	0.41	0.52
Achromatic contrast	7.07×10^1	1.25×10^2	2.00	0.16
Luminance	-3.71×10^{-1}	4.34×10^{-1}	0.01	0.95
Chromatic contrast/achromatic contrast	-1.86	3.25	0.34	0.56
Chromatic contrast/luminance	6.85×10^{-3}	9.30×10^{-3}	0.40	0.53
Achromatic contrast/luminance	3.62×10^{-3}	3.34×10^{-3}	0.94	0.33

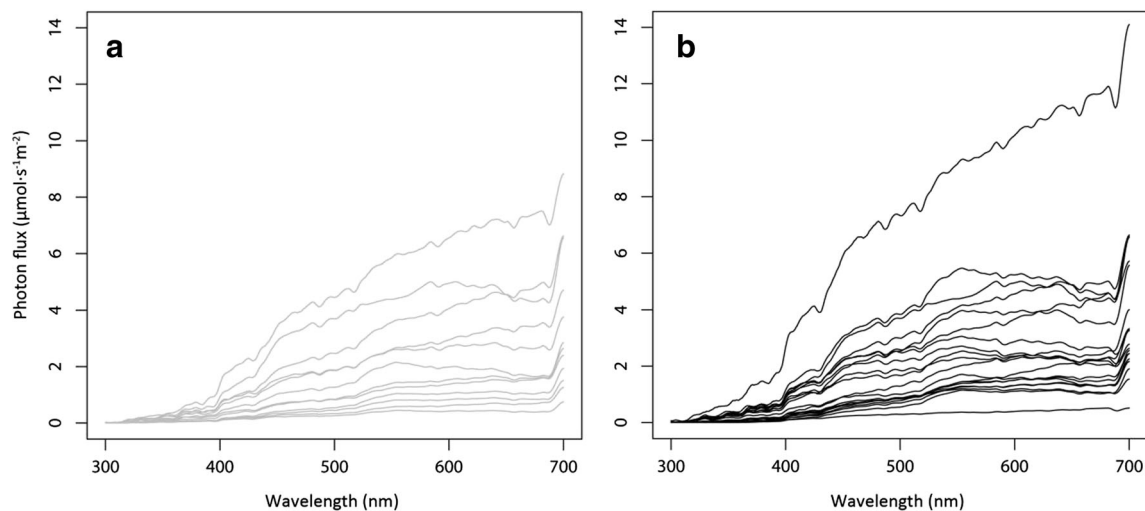


Fig. 2 The photon flux spectra in red bishop nests where the experimental parasitic egg was accepted ($n=12$) (a) or rejected ($n=20$) (b)

From a total number of 24 rejections, in only one case was the nest abandoned and only a single rejection error was recorded, in which parental eggs were rejected instead of parasitic eggs. Both cases were recorded in experiments with real conspecific eggs.

Discussion

In the case of the red bishop, the light environment in domed nests does not appear to make dark eggs more cryptic. This could be explained by the relatively bright light conditions in all red bishop nests; total illuminance did not affect host responses as light conditions were not dim enough to hinder egg discrimination. This could be attributable both to the fact that nests are thin-walled, letting through light (Fig. 3), as well as the lack of shade provided by the surrounding vegetation, comprised largely of cattails. Total illuminance is likely to play a role only in discrimination below threshold values of nest luminosity for colour discrimination, i.e. in scotopic as opposed to photopic light conditions (Węgrzyn et al. 2011). In general, from the perspective of light intensity, red bishop nests are more similar to open nests than cavities, where the amount of light is limited (Langmore et al. 2005, 2009; Węgrzyn et al. 2011) and parasitic eggs can appear to be cryptic (Langmore et al. 2009).

In red bishop nests, the small amount of variation in both chromatic and achromatic contrasts between host and brown eggs indicated that there was very little difference in the light environment between nests. By contrast, in the open-nesting great reed warbler, the interaction between ambient light conditions in the field (where nests are often in shade) and chromatic contrasts predicted rejection behaviour of hosts (Honza et al. 2011). Our results also contrast strikingly with those of Antonov et al. (2011), who experimentally parasitized

the open but dimly lit nests of nightingales *Luscinia megarhynchos* with bright (blue and white, respectively) and dark (green and black, respectively) eggs, and found that bright eggs were rejected more commonly. In red bishops, the reverse is the case: rejection rates for dark eggs were significantly higher than for bright (conspecific) foreign eggs.

The only other measurements of domed nests were recorded by Langmore et al. (2009), who measured eggs of three cuckoos in six species of hosts, five of which have domed nests, and only one, the red-capped robin *Petroica goodenovii*, has an open-cupped nest. They show that dark *Chrysococcyx* eggs are cryptic in domed host nests but that the degree of crypsis depends on the threshold at which colour or brightness cues become more important—about which very little information is available. Luminosity measured in red bishop nests



Fig. 3 Red bishop nest

ranged between 101 and 2650 $\mu\text{mol s}^{-1} \text{m}^2$: the lower point of this range was much greater than that measured in five Australian dome-nesting hosts (0.1–1.6 $\mu\text{mol s}^{-1} \text{m}^2$). By contrast, the nest luminosity they measured for red-capped robins (in which hosts laid mimetic rather than cryptic eggs) was 483 $\mu\text{mol s}^{-1} \text{m}^2$, which falls within the range we recorded for red bishop nests.

Selection pressure from inter-specific parasitism by the diderick cuckoo is potentially considerable, particularly in small colonies such as the ones where we conducted our research, despite the fact that we did not hear or see a cuckoo, nor find any cuckoo eggs, during either field season. This probably reflects relatively low density of cuckoos relative to bishops in our study area (see http://sabap2.adu.org.za/species_info.php?spp=352#menu_left; cf http://sabap2.adu.org.za/species_info.php?spp=808#menu_left). Although of a similar colour to red bishop eggs, diderick cuckoo eggs are considerably larger and are thus easily discernible (Tarboton 2001). In Pietermaritzburg (Kwazulu Natal Province), ca 1800 km northeast of our study area, Lawes and Kirkman (1996) found that only eggs that were heavily maculated or had a darker background colour than the host's light blue eggs were rejected. They conclude that the relatively low rates of rejection (11.1 %) of cuckoo egg models they observed may be a consequence of evolutionary lag in a co-evolutionary arms race between host and parasite.

We suggest that future studies should focus on forest-breeding birds, which may experience variable ambient light conditions and diverse vegetation geometry (Endler 1993). Clearly, more investigation of domed nest-building species is required, as this type of nest appears to have a highly variable light environment, dependent on both nest structure and habitat. But the nest light environment hypothesis may explain some cases in which non-mimetic cuckoo eggs are accepted, thus complementing explanations based on the costs associated with egg discrimination and parasitism risk (Davies et al. 1996), and those that emphasize host age and experience (Lotem et al. 1995; Moskát and Hauber 2007).

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